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## THE CRANIAL ANATOMY OF THE PERMIAN AMPHIBIAN PANTYLUS

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**ABSTRACT.** A detailed description is given of the skull structure of the early Permian tetrapod *Pantylus*, using both whole specimens and a skull serial sectioned and reconstructed in wax plates. This study definitely proves that *Pantylus*, often thought to be a reptile, is a microsaurian amphibian, and furnishes further proof that microsaurians cannot be considered reptilian ancestors.

### INTRODUCTION

*Pantylus*, known in the past mainly from a heavily-built, heart-shaped skull carrying a powerful dentition, is an early Permian tetrapod from the Texas red beds whose systematic position has been open to considerable doubt. Cope, who obtained the first materials of this animal, originally considered it to be a batrachian (1881), but later classed it among the Reptilia (1892, 1896), as did a long series of later workers, including Case (1911, 1912, 1915), Huene (1913), Broom (1913), Williston (1916a, 1916b, 1925), and Wilson (1951). Two decades or so ago, however, in considering the nature of the Paleozoic microsaurians, it became obvious to me that it was, as far as known, basically similar in structure to members of the microsaurian family Gymnarthridae, and hence should be placed in the order Microsauria (Romer, 1950). My conclusion has, I think, been generally accepted by recent workers (cf., for example, Dechaseaux, 1955; Gregory, Peabody, and Price, 1956; Tatarinov, 1964). However, it seems important to add as much as possible to our present inadequate knowledge of its structure in order to attempt to fix its systematic position.

But the importance of such study goes further. Most microsaurians are very poorly known anatomically. If (as I hope to demonstrate) *Pantylus* is a true microsaurian, a study of its cranial structure may prove of value in fixing the phylogenetic position of that group as a whole. Microsaurians have often been claimed to be related to the

captorhinomorph cotylosaurs and to be possibly ancestral to the reptiles, or to at least part of that class (cf., for example, Williston, 1908; Westoll, 1942a, 1942b; Olson, 1947; Huene, 1948; Vaughn, 1960, 1962; Brough and Brough, 1967).

Another possibility that has been suggested is that the microsaur may be ancestral to modern amphibians, particularly the urodeles (Romer, 1950, etc.), although this suggestion is far from generally accepted (cf., for example, Parsons and Williams, 1963). The pedigree of the microsaur is in doubt. I have, since 1933, somewhat arbitrarily combined the microsaur with the aistopods and nectrideans in the Lepospondyli, in an expanded use of that term. But the interrelationships of the three groups are far from certain. And while the derivation of the Labyrinthodontia from the rhipidistian crossopterygians seems clear, there has been little evidence to tie any of the three lepospondyl orders into this evolutionary series.

*Previous studies; materials.* Cope's original materials consisted of two imperfect skulls; from these he was able to describe much of the roof pattern and part of the palate. Later studies of these specimens by Case (1911) and Huene (1913) added little; however, here, as frequently, Broom (1913) was able to give greater depth to analysis of the specimens available to him. Mehl, in 1912, described a fragmentary skull collected for the University of Chicago in 1908 by Paul C. Miller, but added little of interest. The latter collector, in expeditions of 1913 to 1916, obtained a series of specimens, including several skulls and some postcranial materials, from the Mitchell Creek locality; Williston (1916a) described much of this material, giving an adequate account of the skull roof (except the temporal region), some further data on the lower jaw and palate, and a few scattered details regarding the braincase and postcranial skeleton.

No further materials were found until, in 1939, Mr. A. Witte of Henrietta, in charge of a WPA group under the auspices of the Texas Bureau of Economic Geology, came upon a "nest" of specimens near Windthorst, Archer County, Texas; this suite, now entered as No. 40,001 (1-8) in the Texas Memorial Museum, Austin, includes several skulls and considerable postcranial materials. In Mr. Witte's possession is a further small skull from this locality. Post-war trips to Texas from the Harvard Museum of Comparative Zoology (abbreviated as MCZ below) yielded further specimens — two skulls from the Archer City bonebed, a partial skull from Montague County, and two incomplete crania from southern Archer County.

Study of this newer material, together with re-examination of older Chicago specimens, now makes it possible to give a nearly complete account of the skeletal anatomy of *Pantylus*. The post-cranial skeleton is now being studied by Dr. Robert L. Carroll of McGill University. Both Dr. Carroll and I are much indebted to Drs. E. C. Olson and R. Zangerl of Chicago, Drs. John A. Wilson and Wann Langston, Jr., of Austin, and Mr. Witte for the loan of materials. Also, I gratefully acknowledge financial aid for the preparation of material from National Science Foundation Grant GB 500.

For cranial anatomy, some of the older Chicago and American Museum specimens were restudied. Valuable were, as noted, Harvard skulls MCZ 2040 and 3302. The latter is incomplete and broken, but the parts preserved show excellent detail, including some braincase structure. MCZ 2040 is complete, except that the roof is broken off posteriorly on one side. It shows surface structures perfectly, and the break is valuable in that it reveals much of the braincase. Several of the Texas Memorial Museum specimens show aspects of skull anatomy. Most important was No. 40,001 (1), which, with the consent of Prof. John A. Wilson, was serially sectioned and reconstructed, enlarged  $\times 6$ , in wax plates. The surfaces of each section were preserved by the cellulose "peel" method, and at each grinding two peels were taken. Although this sectioned specimen was extremely valuable in revealing internal structure, and is the main "document" on which Figures 3 - 12 are based, it proved disappointing in two regards. (1) Subsequent to burial, it was invaded by calcite, obviously crystallized out of ground water. This crystallization caused multiple small fractures in the skull, which have rendered details of sutures in the dermal bones difficult to determine. (2) Before burial, the skull received one or more violent blows, which, apart from shattering a fraction of the roof (a matter of small moment), jarred loose the vomers, the epipterygoids, the basisphenoid plus parasphenoid, and most of the otico-occipital elements of the braincase. For the most part, these elements are still present in the specimen, lying, disarticulated and more or less battered, between the lower jaws. Their restoration and proper positioning in the braincase and palate presented obvious difficulties. Fortunately, most needed data on these disarticulated or demolished elements are available in MCZ 2040 and 3302.

*Stratigraphy and systematics.* Cope's original specimens were collected by Jacob Boll in 1880 from the "Big Wichita." In his first expedition, two years earlier, Boll had explored no higher in the Texas beds than exposures in the Belle Plains Formation of the

Wichita Group, between the site of the modern Diversion Dam on the Big Wichita River and the exposures along the Little Wichita south of Dundee. In 1880, however, he went somewhat further west, and there is reason to suppose that he collected at the Mitchell Creek locality from which Paul C. Miller later collected many valuable amphibian specimens for S. W. Williston (Romer, 1928, 1935). This locality lies high in the Clyde Formation, very generally regarded as the uppermost formation of the Wichita Group except for the overlying Leuders limestones. Miller's 1908 specimen, described by Mehl, is entered merely as from the "Big Wichita" but is probably from Mitchell Creek. His later materials, described by Williston in 1916, are all definitely from Mitchell Creek.

All the early described specimens, thus, are probably from a single locality and horizon near the summit of the Wichita Group. The newer materials extend the range stratigraphically and topographically. With two exceptions, all are from the Putnam Formation, considerably lower in the Wichita Group (and in early days thought by many to be part of the Cisco Group of the Carboniferous). The Texas Museum specimens, and the individual later collected by Mr. Witte, were found in an exposure in Section 55, Block 3, of the Clark and Plumb Subdivision, about 4 miles north of Windthorst, Archer County; the horizon is about the middle of the Putnam Formation. One Harvard specimen, MCZ 2041, is from the J. J. Prather Survey, about 5 miles northwest of Stoneburg, Montague County; this is at about the same horizon as that of the Texas Museum specimens. Harvard skulls MCZ 2040 and 3302 are from a bonebed about a mile southwest of Archer City, Archer County, which is close to the summit of the Putnam Formation. Two final specimens, MCZ 1913 and 3610, are a poorly preserved skull and a snout fragment from Section 1834, Texas Emigration and Land Co., north of the West Fork of the Trinity River in south-central Archer County and just below the presumed boundary between the Moran Formation and the overlying Putnam. It now appears, hence, that *Pantylus* was in existence for at least most of Wichita time.

Cope's original specimens were given the name *Pantylus cordatus*; no other species properly pertaining to the genus has been described. Cope in 1896 described as *Pantylus coicodus* a fragmentary specimen, mainly a tooth row, from Coffee Creek in the Arroyo Formation of the Clear Fork Group. However, these teeth are bulbous, pointed structures, quite unlike those of other *Pantylus* specimens. As various later writers have noted, they do not appear to belong to *Pantylus* (Case, 1911; Gregory *et al.*, 1956), and the specimen is

perhaps a caseid. A jaw fragment from Coffee Creek to which Cope gave the manuscript name *Pantylus tryptichus* is probably a captorhinid (Cummins, 1908; Case, 1911; Gregory *et al.*, 1956). Williston in 1913 gave the name *Ostodolepis brevispinatus* to a series of small vertebrae from Coffee Creek. In 1916 he noted the similarity of these vertebrae to those of *Pantylus*. "*Ostodolepis*," as described by Case (1929), is a gymnarthrid microsauro of a different nature, but as noted by Carroll and Baird (1968), there is no guarantee that Case's specimen is related to the type.

It is possible that the stratigraphically lower Putnam and Moran materials are specifically distinct from the earlier described specimens from the Clyde. There is some variation in skull size, in general amounting to about 20 per cent, most skulls ranging in measured or estimated length from 72 to 90 mm; but this variation may be related to age or sex. The Witte specimen has an estimated length of about 36 mm, and one Chicago specimen from Mitchell Creek is but 39 mm long; but these are surely young individuals, presumably conspecific with the larger individuals found with them. There are dental differences, in the description and figures of earlier writers, regarding the number of teeth in the marginal rows, noted later, and the pattern of toothplate teeth. But one may strongly suspect that the patterns figured are in some cases diagrammatic and not entirely trustworthy. Quite surely age (and sex?) factors enter into variations in toothplate dentition. There may be individual differences, as well. For example, the skull sectioned by me has a large central tooth in both upper and lower toothplates, but Williston mentions a specimen in which such a tooth was present above but not below, and figures (how accurate I do not know) of other specimens show no such enlarged tooth in either upper or lower dentition.

### DESCRIPTION

*Skull roof* (Figs. 1, 2, 7, 12). The skull of *Pantylus* is very massively built, and very broad and low — its width, which, from a rounded snout, spreads out greatly in the cheek region, is nearly as great as the length. There is no otic notch. The cheek in the jugal region extends downward so as to cover externally a considerable area of the lower jaw. Skull height, even allowing for the depth of the overhanging cheek region, is little more than a third of the length. The broad roof is nearly flat, although bending sharply downward at the margins of the "table," and there is a somewhat overhanging snout. The roof bears, as in most early or primitive

amphibians, patterns of ridges and intervening valleys radiating from the ossification centers of the dermal elements. There is no evidence of grooving for lateral line canals. The small skull in Mr. Witte's collection shows nearly straight sutures between roofing

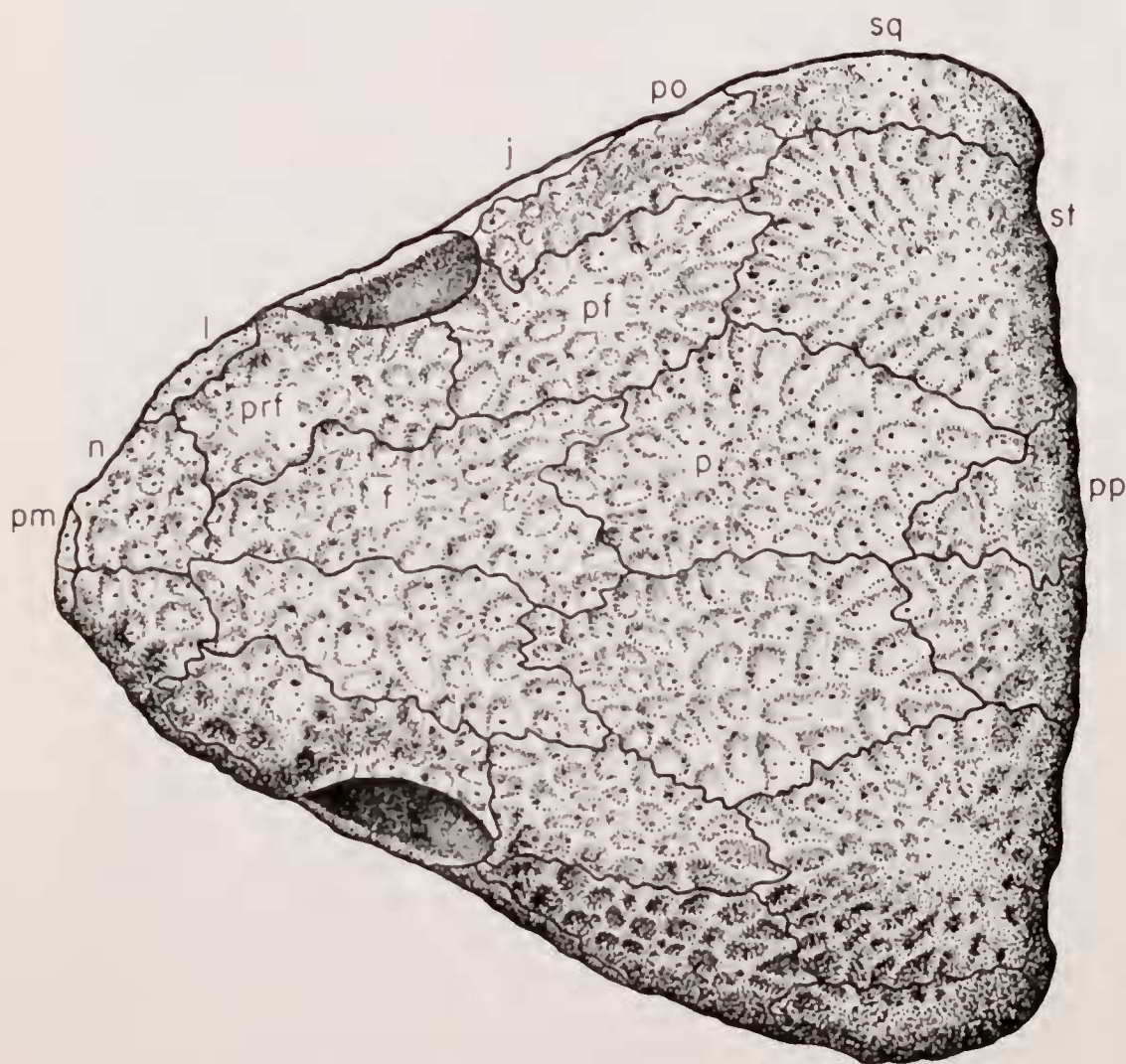


Fig. 1. Dorsal surface of skull, based on MCZ 2040; right posterior area restored,  $\times 1\frac{1}{2}$ . Abbreviations for this and following figures: *a*, angular; *ar*, articular; *asp*, anterior splenial; *ba*, basal articulation of braincase with palatal structures; *bo*, basioccipital; *bs*, basisphenoid; *c*, coronoid; *ch*, choana; *d*, dentary; *e*, epipterygoid; *en*, external naris; *eo*, exoccipital; *f*, frontal; *fo*, fenestra ovalis; *fv*, foramen for transverse vein in pituitary region; *j*, jugal; *l*, lacrimal; *m*, maxilla; *n*, nasal; *op*, opisthotic; *p*, parietal; *pal*, palatine; *par*, prearticular; *pf*, postfrontal; *pm*, premaxilla; *po*, postorbital; *pp*, postparietal; *pr*, prootic; *prf*, prefrontal; *ps*, parasphenoid; *psp*, posterior splenial; *pt*, pterygoid; *q*, quadrate; *qj*, quadratojugal; *sa*, surangular; *se*, sphenethmoid; *sm*, septomaxilla; *soc*, supraoccipital; *sq*, squamosal; *st*, supratemporal; *v*, vomer; *I, II, V, X*, foramina for cranial nerves.

elements. With growth, however, the superficial portions of the roofing bones tend to interosculate, producing, as generally in Paleozoic amphibians, a series of zig-zag sutures. For the most part, the pattern is a bilaterally symmetrical one, although (as generally) four-square meetings of bones are not to be found. However, in the skull figured, the right frontal has invaded and taken over an area properly belonging to the right parietal.

The premaxilla is thick extero-internally, but short; it covers mainly the "overhang" anteriorly leading down to the tooth row between the external nares. It extends backward laterally below the naris to include the region of the base of the lateral premaxillary teeth. The nasals are likewise short, but broad, extending down laterally to the upper border of the nares. Frontals and parietals are long. There is no parietal foramen.

The external naris, facing laterally, is large and subcircular in outline. The premaxilla forms most of its anterior border, the maxilla the lower margin, the nasal the upper boundary, while the lacrimal extends broadly forward to a point close to the posterior margin. However, the lacrimal and, to a lesser extent, the maxilla and nasal are excluded from the narial margin by a highly-developed septomaxilla. This forms a narrow external rim along the posterior half of the narial opening and then turns inward to form a posterior wall and partial floor and medial wall to the nasal passage inside the narial opening. Evidently the air passage turned sharply upward inside the external narial opening to reach a dorsally placed nasal capsule. The anterior opening of the lacrimal duct pierces the septomaxilla just internal to the narial opening.

The lacrimal is well developed, extending from the orbit to the narial region; ventrally it is overlapped to some degree by the maxilla, but dorsally it extends high up on the side of the face, and posteriorly it extends, in a slender process, well back to a point below the orbit. Sections (Fig. 3) show that the lacrimal is essentially a cylindrical mass of bone surrounding the lacrimal duct and is, so to speak, cradled below by the maxilla. The thickness of the lacrimal bone produces a swelling of the generally smooth internal surface of the dermal roof anterior to the orbit; this swelling is continuous with a thickened anterior margin of the orbit which extends upward and backward along the prefrontal. The posterior opening of the lacrimal duct lies just inside the orbital margin.

The orbit, facing essentially laterally, is a large and somewhat oval opening, its highest point being considerably posterior to the lowest point in its ventral margin. The prefrontal is well developed, occupying a large portion of the extended dorsal and anterodorsal

margins of the orbit; dorsally it extends forward between frontal and lacrimal to reach the nasal. The postfrontal, abutting posteriorly on the prefrontal, is large and extends far backward lateral to the frontal and parietal; it has, however, only a very short posterodorsal boundary on the rim of the orbit. The postorbital is likewise highly developed and elongate, the postfrontal and postorbital between them occupying much of the area which in labyrinthodonts is occupied by the "temporal" elements. The arrangement along the orbital margin is of interest. The postfrontal (as in

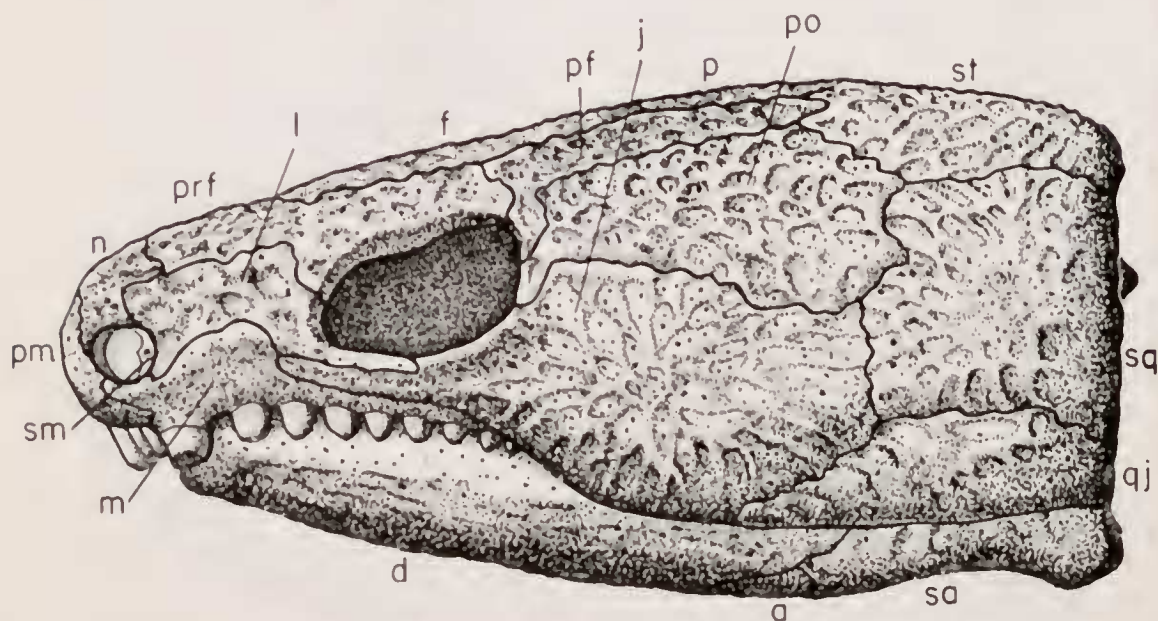


Fig. 2. Lateral view of skull and jaw, based on MCZ 2040,  $\times 1\frac{1}{2}$ .

*Tuditatus*) pushes downward posteriorly to take over a portion of the orbital margin which should properly be occupied by the postorbital; the latter bone, in turn, extends downward along the orbital margin to encroach upon the area properly pertaining to the jugal. A thickened ridge runs downward and forward inside the posterior orbital margin along the postorbital and jugal.

The jugal is a very large bone. It borders the posterior portion of the lower orbital margin, and sends a narrow extension far forward between lacrimal above and maxilla below. Back of the orbit it occupies a broad expanse of cheek, and forms most of a prominent flange extending downward, external to the posterior end of the tooth row and concealing the upper part of the lower jaw posteriorly.

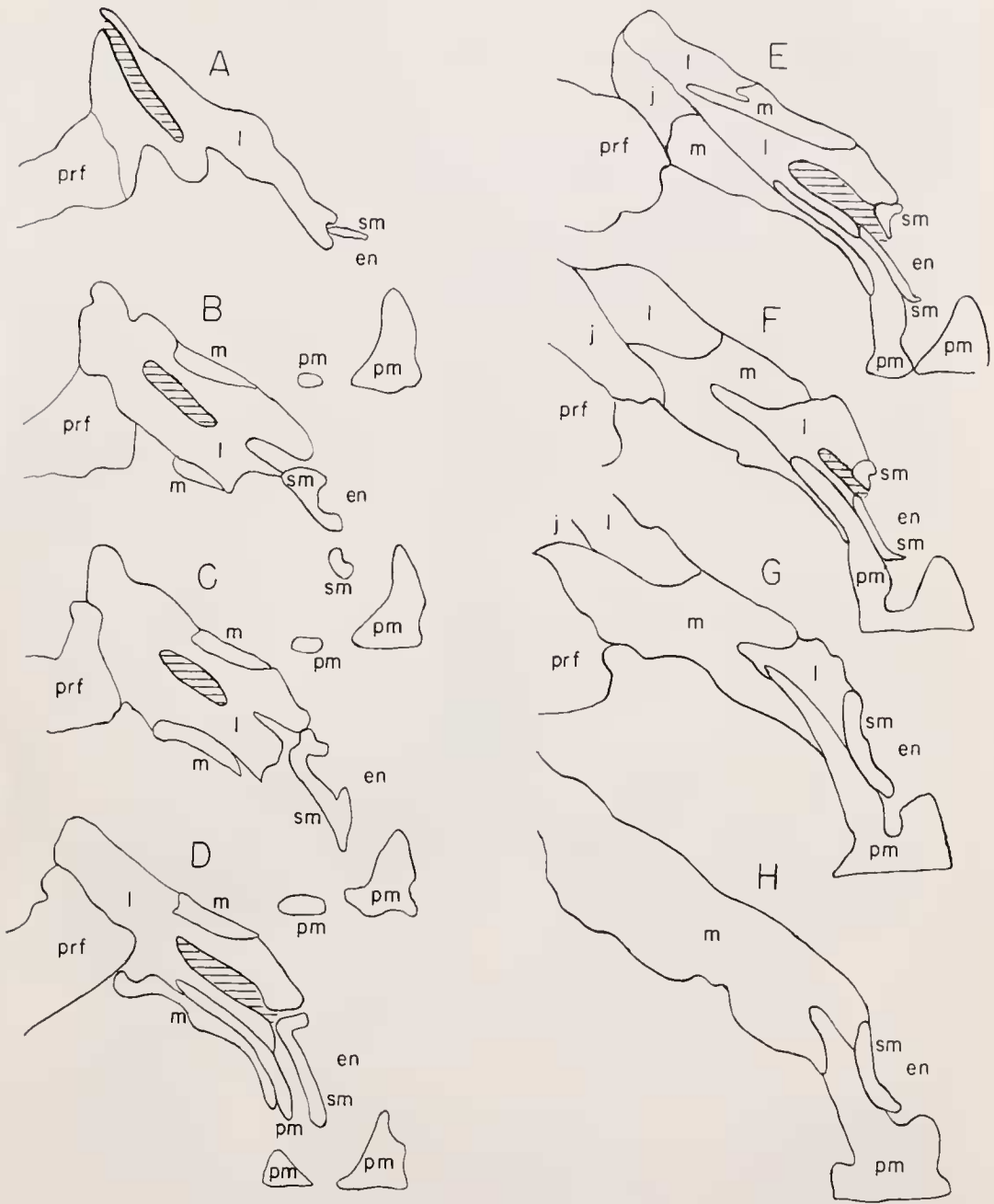


Fig. 3. A series of sections, in a horizontal plane, of the region anterior to the left orbit, in dorsoventral order, to show the relations of the lacrimal duct to the surrounding bones. From the sectioned skull,  $\times 3$ . The lacrimal duct is hatched. The duct is seen leaving the orbit in section A; by E it enters the narial area through a foramen in the septomaxilla, which forms posterior and medial walls to the naris. From B downward, the maxilla is seen to bound the lacrimal medially as well as laterally.

The maxilla is stout mediolaterally, to contain the roots of the marginal teeth, but has only a limited facial exposure, except anteriorly above the large "canine." It is partly excluded from the naris by the septomaxilla, rimming it only for a short distance between premaxilla and lacrimal. Posteriorly, at the end of the lateral tooth row, the maxilla is covered externally by the jugal.

The posterior rim of the skull roof is formed by the paired postparietals, "supratemporals," squamosals, and quadratojugals. This series, as noted below, extends broadly on to the occipital surface. The postparietals are of modest size and are somewhat triangular in shape, in dorsal view, narrowing anteriorly. The large bone that may be provisionally termed the "supratemporal" is bounded by the postparietal and parietal medially, the squamosal and postorbital laterally, thus occupying essentially the position of the tabular and

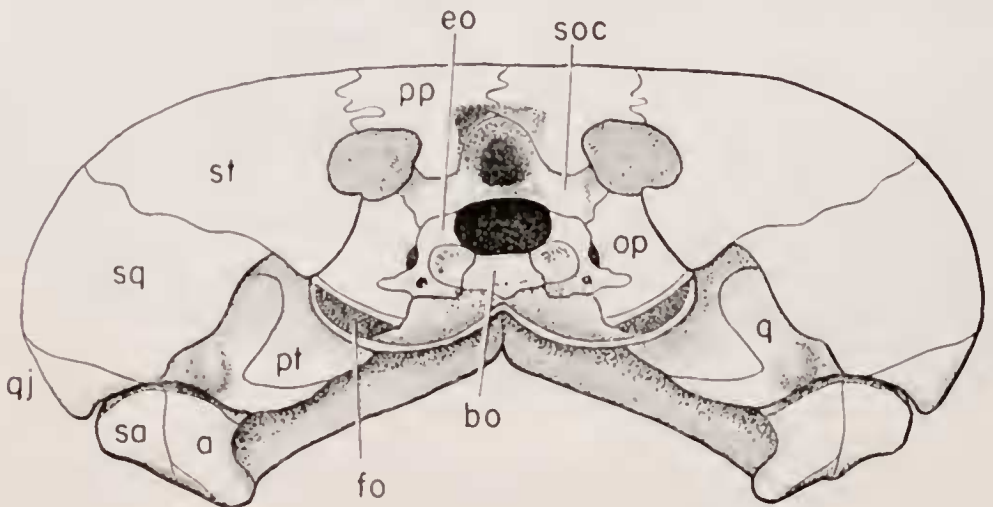


Fig. 4. Posterior view of skull, based mainly on MCZ 2040,  $\times 1\frac{1}{2}$ .

supratemporal of labyrinthodonts; it is in contact anteriorly with the postfrontal. The squamosal is likewise of considerable size in external exposure. The quadratojugal extends well forward along the lower margin of the cheek flange formed more anteriorly by the jugal; externally, it is narrow dorsoventrally, but the sectioned skull indicates that it underlaps the squamosal to a considerable degree internally. As noted below, it turns inward posteriorly to take part in the jaw joint.

*Palate* (Figs. 4, 5; 8-11 in part). Part of the palate could be made out in earlier described specimens. In the sectioned specimen, nearly the entire palatal structure can be accurately determined. The epipterygoids and vomers were disarticulated post-mortem; however, these structures were found preserved between

the lower jaws and could be readily restored to position.

The pterygoids are always long and highly developed in primitive tetrapods; here, the development is exceptional, for they extend almost the entire length of the skull. Anterior to the area of the basal articulation there is a narrow interpterygoid vacuity; this, however, extends forward little more than half the distance from basal articulation to naris. Anterior to this point, the two pterygoids meet in a median suture; this suture is of some thickness between the anterior halves of the palatines, but thins between the nares. Anterior to the region of the basal articulation, the pterygoids, as seen in ventral view, appear as a pair of rounded ridges, which bear two or three irregular rows of small teeth and are separated by a deep groove from the palatines lateral to them. Anteriorly, these ridges gradually narrow but continue to bear teeth to a point between the vomers, rather forward of the level of the posterior margins of the nares.

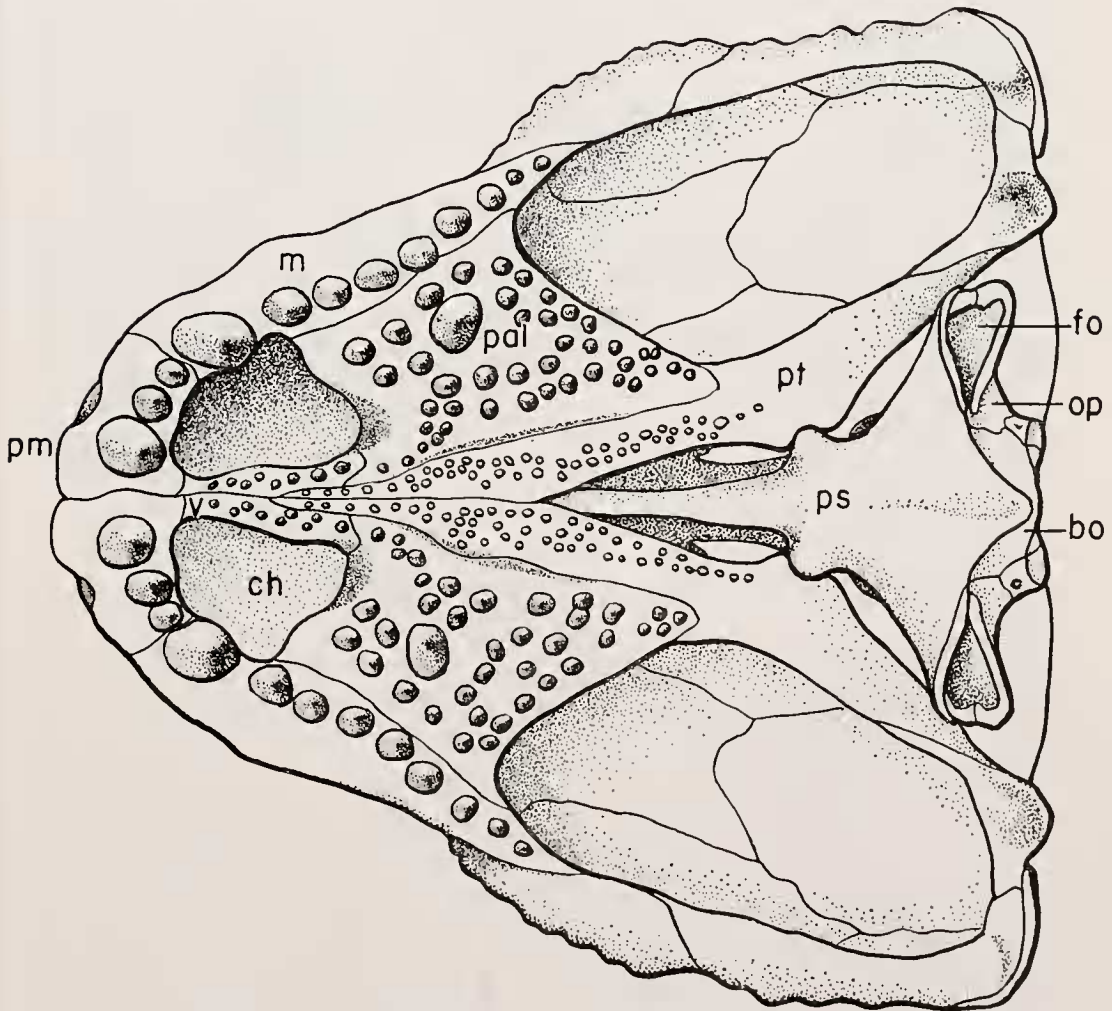


Fig. 5. Palatal view of skull, based on the sectioned specimen,  $\times 1\frac{1}{2}$ .

The tooth-bearing surface of this most anterior region was broken off, together with the vomers, in the sectioned skull; but as preserved, the specimen shows a further forward continuation of the pterygoids dorsally as a pair of narrow but obviously stout little rods which reach nearly to the level of the anterior margins of the nares. For most of the broad palate, the pterygoids are covered ventrally, lateral to their median ridges, by the palatines; in dorsal view, however, the pterygoids are seen to extend laterally above (and to strengthen) the palatines, to gain contact laterally with the jugals. I have found no sutural evidence for the presence of an ectopterygoid, although such a bone may have persisted in an area internal to the posterior rim of the orbit.

The bony choanal openings are very large. They are separated from one another only by the narrow vomers, with, above them, the anterior tips of the pterygoids. Anteriorly and laterally they reach close to the bases of the premaxillary and anterior maxillary teeth, and are bounded posteriorly by the curved anterior margins of the palatines. Only the posterior parts of these openings, however, are truly choanal, for (as shown by the sectioned specimen) the large anterior teeth of the lower jaw extended upward into the anterior part of these openings when the jaws were closed.

The vomers were displaced in the sectioned skull, but other specimens show them in proper position. They are narrow tooth-bearing elements bounding the choanae medially. They are appressed medially to the slender anterior ends of the pterygoids, except that anteriorly the two vomers are in contact ventrally below the tips of the pterygoids. Anteriorly, the vomers articulate with the premaxillae; this articulation, however, is well above the level of the rim of the upper jaw; stout paired processes of the premaxillae rise dorsoposteriorly to make this contact (Figs. 8-11).

The palatines, in correlation with the powerful dentition they bear, are greatly expanded as essentially quadrilateral plates. Medially the palatine is separated from the pterygoid on the ventral surface by a longitudinal groove, deep anteriorly but fading posteriorly. The anterior, choanal, border is concave in outline. Medially the anterior margin of the bone is somewhat convex ventrally in transverse section, forming a ridge continued anteriorly by the vomer. Lateral to this, the surface is somewhat concave ventrally at the choanal margin, the concavity fading out posteriorly. Posteriorly the margin is concave in outline, the medial margin extending well posteriorly, underlain dorsally by the pterygoid. There is no development of the transverse pterygoid flange characteristic of all primitive reptiles.

Approaching, posteriorly, the region of the basal articulation, the pterygoid, as in all primitive tetrapods, narrows in transverse width and twists to a vertical plane, to form the quadrate ramus of the bone. Just in front of the articular region it sends upward a sharp spur, which aids in the support of the epipterygoid. Behind this spur the upper edge of the pterygoid is gently concave on its medial aspect, to form the lower part of the articular surface for the basipterygoid process. The posterior, quadrate ramus of the pterygoid rapidly develops into an extensive plate, thin from side to side

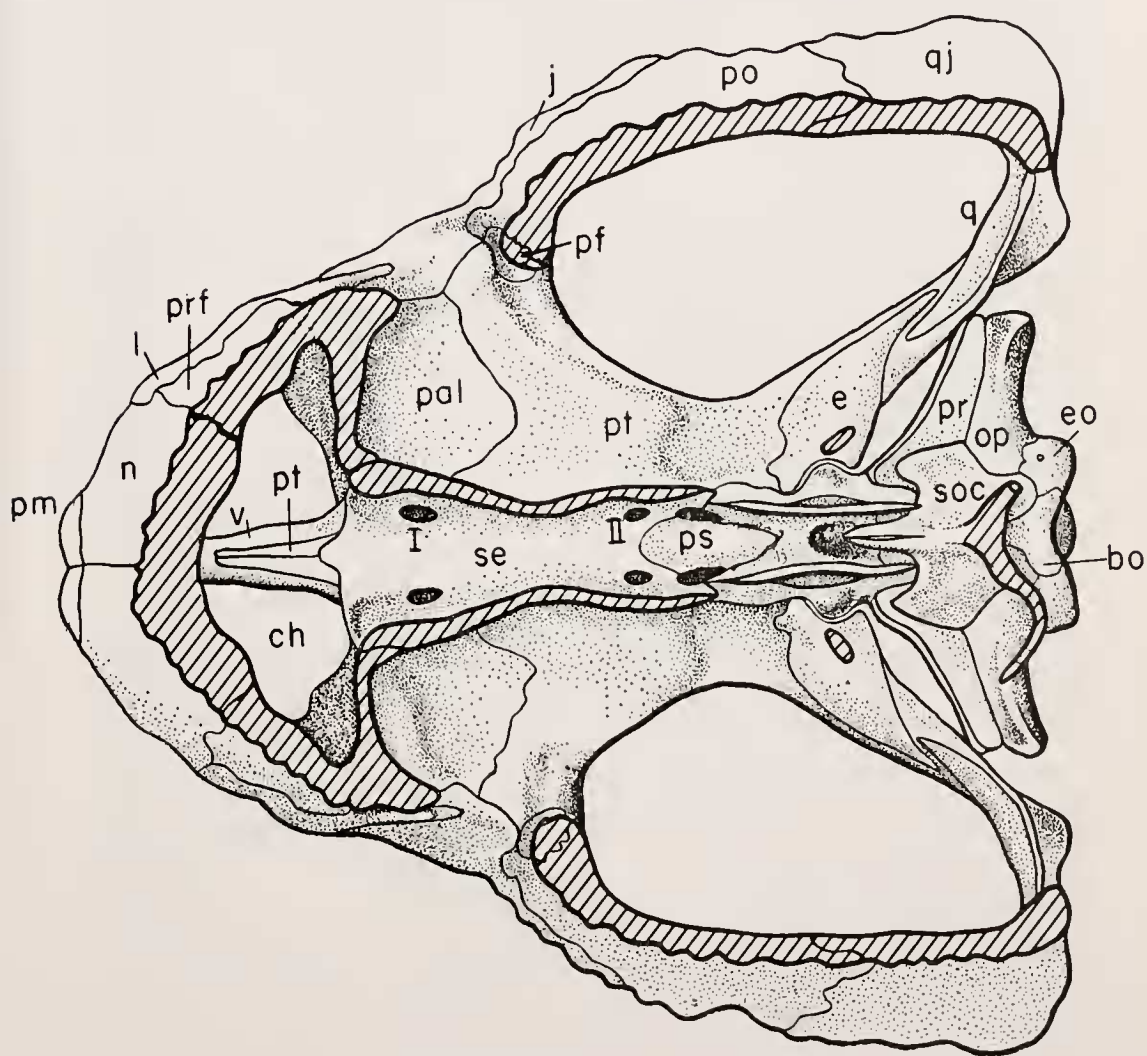


Fig. 6. Skull roof diagrammatically removed to show palate from above. Dermal roof sectioned horizontally through level of middle height of orbit; sphenethmoid and ascending ramus of epipterygoid sectioned at same level, but dorsal flange of sphenoid complete. Postparietals and tabular removed; supraoccipital shown as complete except for removal of dorsolateral flange on right; based on sectioned specimen,  $\times 1\frac{1}{2}$ .

but of considerable height. It extends ventrally to about the level of the bottom of the cheek flange of the jugal and quadratojugal, and runs back nearly to the region of the jaw articulation. Above this posteroventral point, it contracts somewhat in posterior extent; meanwhile, however, the dorsal margin of the ramus has risen rapidly, and the upper blade of the ramus extends far upward, backward, and laterally, to terminate high up within the temporal region, close to, but not in direct contact with, the squamosal.

The epipterygoids had been jarred loose in the sectioned specimen and had fallen down between the jaws, where they lodged with but little damage. They can be replaced without difficulty in approximately natural position, although with some slight doubt as to dorsal orientation. Below, the bone is expanded into a flat plate

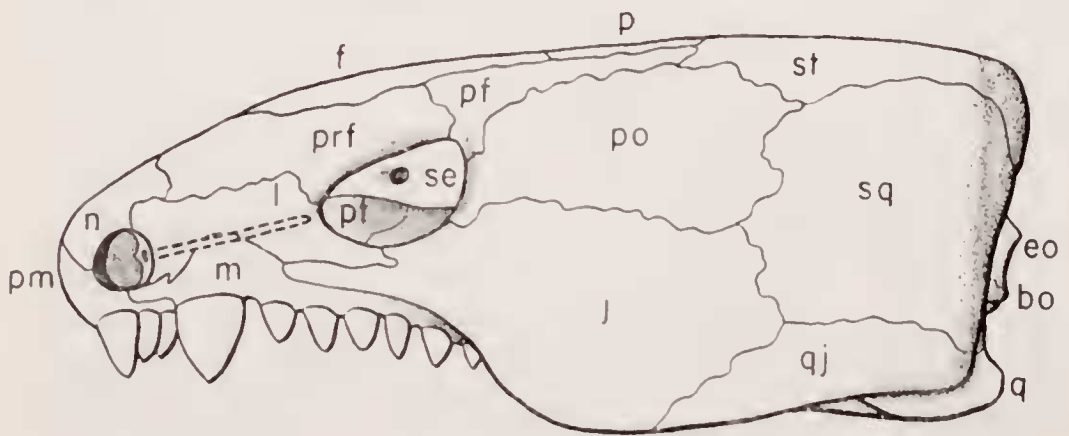


Fig. 7. First of a series of "dissections" in lateral view, based on the sectioned skull. This figure comparable to Fig. 2. The course of the lacrimal duct is shown in broken line.  $\times 1\frac{1}{2}$ .

applied closely to the lateral surface of the quadrate ramus of the pterygoid over a considerable area, mainly below and posterior to the basal articular area and extending only modestly anterior to that point. At the level of the upper margin of the pterygoid, the epipterygoid thickens considerably; a pair of ridges extends medially to form a socket for much of the basipterygoid process. The anterior margin of the bone here is notched to receive the supporting spur of the pterygoid mentioned above. Dorsally, the bone slims out to a slender blade, which reaches far toward the skull roof.

The quadrate is well developed. The articular surface for the lower jaw is broad mediolaterally, relatively narrow anteroposteriorly, and but slightly convex. The quadratojugal turns medially in a flange which is of considerable thickness ventrally; on its lower

surface this forms approximately a third of the articular area. Above the articulation, the quadrate is thickened but gradually thins dorsally. Medial to the articulation, the quadrate is very stoutly developed and extends ventrally and posteriorly beyond the ventral and posterior limits of the "roofing" bones. There is a postero-medial swelling just above the articular region, presumably for a muscular or tendinous attachment. Anteriorly, the quadrate forms a very extensive plate applied closely to the outer surface of the pterygoid and extending far forward toward the epipterygoid. Dorsally, the plate, with the accompanying pterygoid, reaches far dorsally and posteriorly beneath the squamosal.

*Occipital surface* (Fig. 4). In the absence of an otic notch, the skull roof exhibits in posterior view an even, essentially semi-circular, curved margin. In contrast to conditions in most lower tetrapods is the great extension onto the occipital surface of the posterior elements of the dermal roof. The postparietals send a flange of modest size down over part of the supraoccipital on either side. The "supratemporal" sends a broad sheet of bone downward and medially; in the fashion of a labyrinthodont tabular, there is an articulation of the supratemporal with the otic region of the braincase. The attachment is a broad one, meeting both prootic and opisthotic above the fenestra ovalis, and is far more ventrally placed than that of a typical labyrinthodont. There is a normal posttemporal fenestra, bounded mainly by "supratemporal" and postparietal, but ventrally and ventromedially by the otic elements and, to a slight degree medioventrally, the supraoccipital.

Much in the fashion of the "supratemporal," the squamosal sends a broad, thin sheet of bone downward and medially over a considerable lateral area of the occipital surface. Dorsally, this sheet underlies the occipital flange of the "supratemporal" to some extent; ventrally it sheathes the occipital surface of the quadratojugal. It ends freely ventromedially.

Centrally, on the occipital surface is seen the posterior aspect of the braincase. The usual ring of occipital elements — supra-, basi-, and small, paired exoccipitals — surrounds the foramen magnum. Above the foramen magnum the supraoccipital is deeply excavated by a pit, presumably for ligamentous connection with the column. The otic capsule is seen to extend outward far laterally (somewhat as in *Seymouria*) rather than dorsolaterally, as in the paroccipital process of typical labyrinthodonts. Beneath the lateral part of this process the fenestra ovalis is visible; more medially, between opisthotic and a lateral extension of the exoccipital, is the jugular foramen for the vagus nerve (as well as, presumably, nerve IX and the

"jugular" vein). A hypoglossal foramen is present ventrally, and possibly a second hypoglossal opening may be present more dorsally. The occipital condyle is a broad, somewhat concave, and essentially tripartite structure comparable to that of such rhachitomes as *Eryops*.

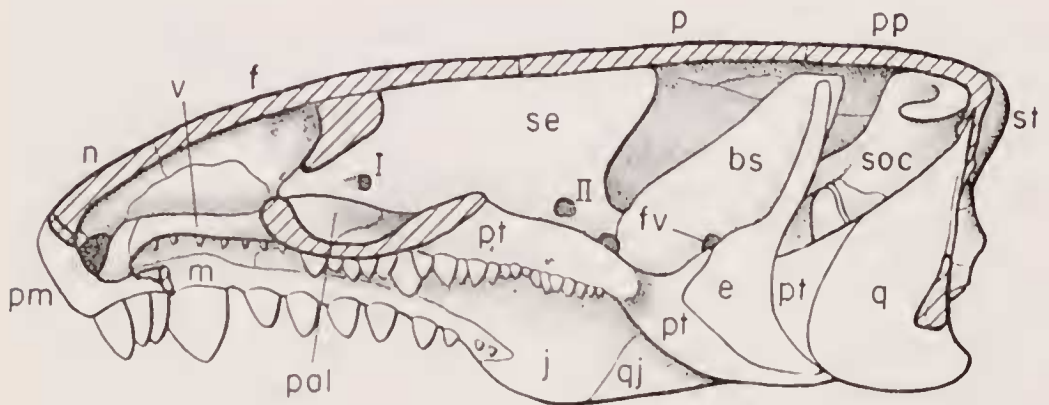


Fig. 8. As Fig. 7, but dermal bone of left side removed (except for premaxilla), to show the palatal structures in lateral view. Sutures with bones removed indicated by hatched areas. At anterior end of sphenethmoid is seen the lateral process of that bone, which is tightly fused to prefrontal; below are shown the surfaces of palatine and pterygoid, which join the lacrimal and jugal. Posteriorly is seen the area of contact between quadratojugal and quadrate.

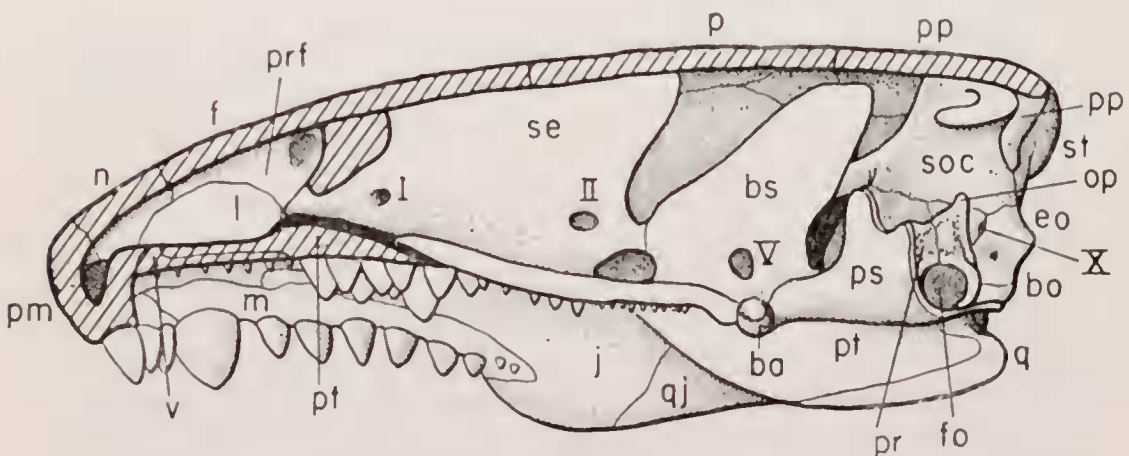


Fig. 9. As Fig. 8, but palatal structures of left side and left premaxilla removed to show lateral view of braincase. Below the anterior part of the sphenethmoid and to the front are seen the medial contacts between the pterygoids and vomers and the ascending processes of the premaxillae, which meet the vomers. The rugose area on the otic bones above the fenestra ovalis is the area of contact with the "supratemporal."

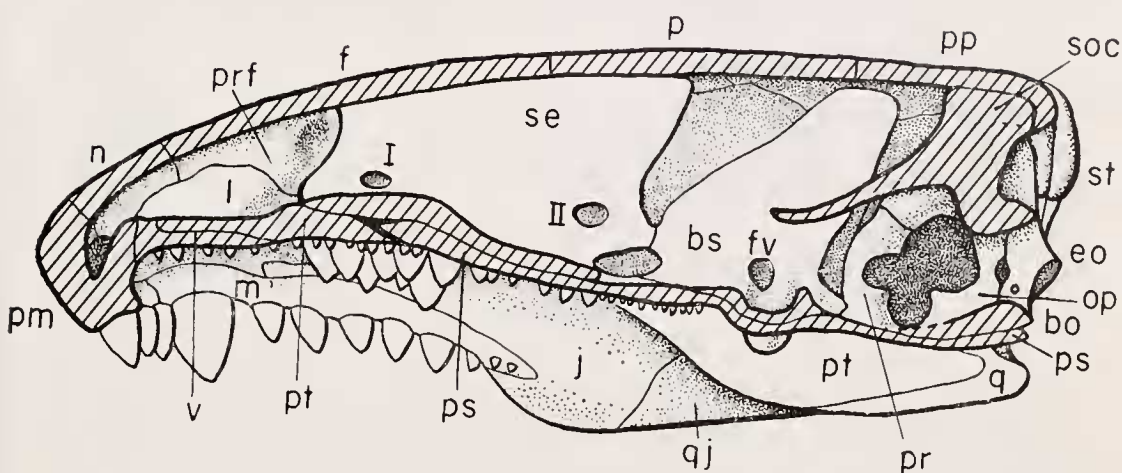


Fig. 10. As Fig. 9, but sectioned through middle of braincase, to show internal structure. Inner surface in otic region restored with doubt.

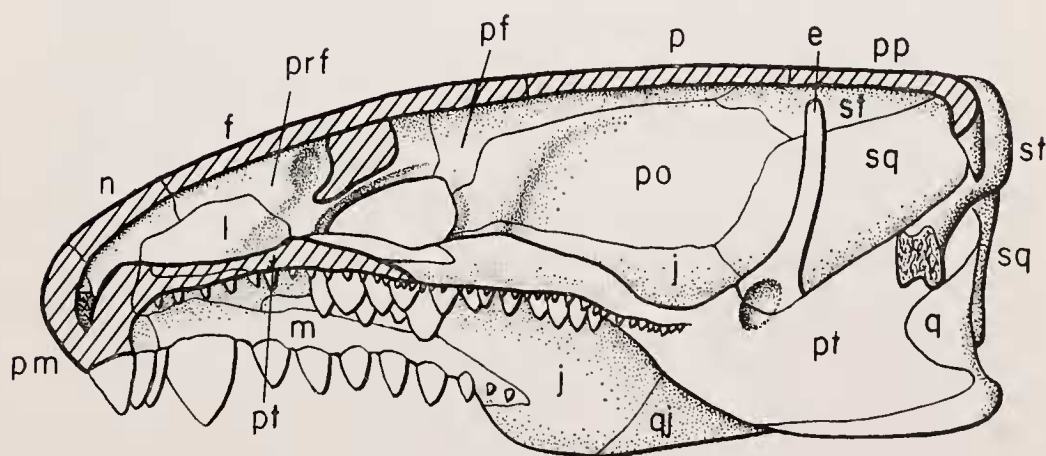


Fig. 11. As Fig. 10, but braincase removed, showing inner surface of right palatal complex. Anterodorsal to orbit is seen the area of contact of the prefrontal with the lateral flange at the front end of the sphenethmoid. A rugose area posteriorly is the sutural surface of the "supratemporal" articulating with the otic elements of the braincase.

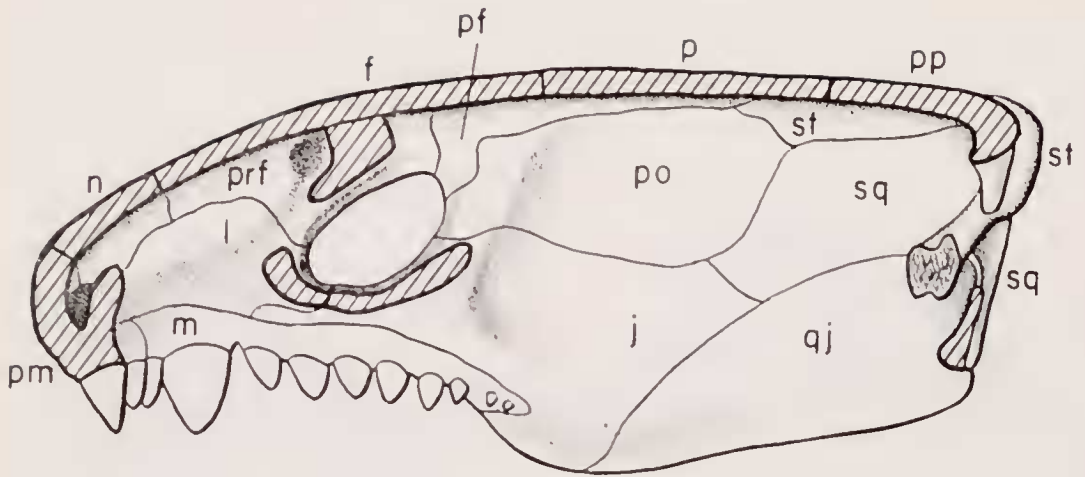


Fig. 12. As Fig. 11, but palatal elements removed, showing the inner surface of the dermal roofing elements of the right side. Posteroventrally is seen the area of contact of the quadratojugal with the quadrate.

*Braincase* (Figs. 4-6, 9, 10). The nasal capsule was unossified. As noted earlier, the external narial cavity is bounded posteriorly and medially by the septomaxilla. Behind this bone, the anterior part of the choanal opening was occupied by the large anterior lower teeth; it is hence obvious that the air passage ascended dorsally from the external naris and that the nasal capsules were dorsally placed, anterolateral to the front end of the sphenethmoid. Beginning anteriorly at about the level of the posterior margins of the choanae, and extending back to about the level of the posterior margins of the orbits, there is a well-developed sphenethmoid. The entire structure is a single ossification, essentially V-shaped in cross section. The ventral edge of the bone is keeled, and in life lay for most of its length in a groove on the upper surface of the parasphenoid rostrum; there is here a stout union between the two thin ascending flanges. These diverge from one another at a modest angle, and then approach each other to a slight degree dorsally. The cavity of the sphenethmoid is widely open both anteriorly and posteriorly. Laterally, opposite the orbit, there is on either side a foramen of considerable size through which the olfactory nerve presumably passed; a second large foramen, presumably for nerve II, lies toward the back end of the bone. Possibly the sphenethmoid may have been penetrated by small foramina for one or more of the eye-muscle nerves, but I have not been able to detect them in the sectioned specimen, and they may have emerged posterior to the sphenethmoid. The sphenethmoidal plates appear to have extended upward to the under side of the roofing elements, but I have not

been able in the sections to determine the exact relations here (Williston, 1916a, fig. 25, shows sections in this region). On either side in front of the orbital rim the prefrontal sends in a powerful medial flange, broadening dorsally, which articulates strongly with the outer surface of the sphenethmoid near its anterior end.

The parasphenoid-sphenoid complex in the sectioned specimen was jolted out of position before burial; present between the lower jaws, it has undergone little damage except for the posterior margins of the parasphenoid (which, however, are preserved in other specimens). It can be replaced fairly accurately in its proper place in the figures because of the known position of the basal articulations and because it can be seen in place in lateral view in MCZ 2040. The anterior portion of the complex is a long parasphenoidal rostrum; a dorsal groove obviously received the ventral keel of the sphenethmoid in normal fashion. Posteriorly, the keel expands gradually and then abruptly produces ventrolaterally a pair of well-developed basiptyergoid processes with stoutly rounded heads that fit into the sockets formed jointly by the epiptyergoids and ptyergoids.

In this region, the complex includes, inside the superficial parasphenoidal dermal component, spongy endochondral bone representing the basisphenoid; endochondral bone is included in the structure of the basiptyergoid process. There is a distinct rounded medial pocket in the basisphenoid opposite the basiptyergoid processes, obviously lodging the pituitary. A distinct crossridge behind the cavity represents the dorsum sellae; behind this point endochondral bone is absent. As in early tetrapods generally, it seems, there was a ventral gap in endochondral braincase ossification between the sphenoid and otico-occipital braincase elements. A pair of small foramina, presumably for internal carotid arteries, penetrates the bone from the under side opposite the posterior margin of the pituitary fossa. A remarkable feature is the presence of extensive wings extending far upward from the basisphenoid and continuous with it on either side; the type of ossification is such as to indicate their endochondral nature. They appear to represent the *pila antotica* of the embryonic braincase. Near the base of either flange is a good-sized foramen that presumably carried the transverse pituitary vein, as in the basisphenoid of various lower tetrapods. Although, as said above, the parasphenoid-basisphenoid can be replaced in a position close to that which it must have occupied in life, there is a degree of uncertainty as to the exact posture of these dorsal flanges. They certainly stopped short dorsally well below the level of the skull roof. In the sectioned specimen the

sphenoid had broken loose from the sphenethmoid, but the two are seen in natural relationship in lateral view in MCZ 2040. Here there is seen a short area of connection between the ascending flanges and the sphenethmoid part way up the side, leaving a gap dorsally and a rounded foramen ventrally. Possibly small eye-muscle nerves emerged above; below is perhaps the point of exit of the profundus branch of nerve V, the more posterior rami of this nerve and nerve VII making their exits behind the dorsal flange of the sphenoid.

It was hoped that the sectioned specimen would show the otico-occipital elements in place. This was not the case. The supraoccipital remained essentially in position, but the other elements had been jarred loose before burial (suggesting, although we appear to be dealing with an adult, rather loose suturing of elements). Fortunately, much of the structure could be made out from MCZ 2040 and MCZ 3302. Dorsoposteriorly, the supraoccipital is firmly fused to the overlying postparietals; in addition, the latter bones, as noted earlier, partially sheath the supraoccipital posteriorly. A narrow process extends dorsolaterally toward the "supratemporal." On either side, the supraoccipital descends and expands to gain contact with the two otic elements and, posteriorly, with the exoccipital. The sections show that, as commonly, the supraoccipital encloses the upper part of both vertical canals of the internal ear, as well as the crus commune. Dorsally, the supraoccipital sends forward an anterior process. One would have expected this to run forward dorsally beneath the skull roof, as, for example, in many reptiles. This is not the case; it slants strongly downward, to terminate anteriorly at about the level of the pituitary rather below half the distance from the skull roof to the braincase floor and between the two ascending flanges of the sphenoid. Uniquely among known early tetrapods, this anterior extension is a dual structure, consisting of two closely apposed narrow rods. As is known from the developmental story in lower tetrapods, supraoccipital ossification takes place in a cartilaginous area formed by dorsal fusion of extensions upward of the two otic capsules; the situation here suggests that the fusion of the two was imperfect.

The exoccipitals are, as usual in early tetrapods, small elements, hung below the supraoccipital on either side. Between opisthotic and exoccipital is a typical jugular foramen. Ventrally, the exoccipitals form the lateral portion of the broad occipital condyle. The basioccipital is a wedge-shaped element, forming the central part of the condyle and tapering anteriorly on the braincase floor.

The pro- and opisthotics jointly form a pronounced lateral extension of the otic region (Fig. 5), tipped at its end by a broad area of articulation with the "supratemporal," somewhat after the fashion of the typical paroccipital process of many early tetrapods (which, however, articulates with the tabular). Below this articular area is the good-sized fenestra ovalis, bounded posteriorly by the opisthotic, anteriorly by the parasphenoid. This latter dermal element covers most of the surface of the prootic, except dorsally, and likewise sheathes the opisthotic ventrally. Parasphenoid and otic elements were apparently not bound closely together in life, since they have cleanly separated in the sectioned specimen. Dorsally the two otic structures are articulated with the supraoccipital. On the dorsal surface of the lateral otic process the suture between pro- and opisthotics lies in a deep groove; obviously the suture between the two was a comparatively loose one (as confirmed by their separation in the sectioned specimen).

In the sectioned skull, three isolated otic elements are clearly seen, but I must confess myself baffled in attempts to interpret them and orient them in a reconstruction. Two of the three, obviously a pair, have, crudely, the shape of a clam shell; the curved outer surface is smooth except for a ridge indicating the division between a free surface and that sheathed by the parasphenoid. The inner aspect, presumably housing part of the internal ear, shows some slight development of ossification. Attached to one of the two is a small area of ossified tissue which presumably represents an exoccipital; in consequence, I interpret the two as opisthotics. By elimination, the third element preserved is a prootic. Here again, the presumed external surface is featureless except for a ridge which may have separated a free dorsal surface from that sheathed by the parasphenoid. On the inner surface there is a considerable degree of ossification in a complex pattern which, however, I fail to interpret. As a result, I can give no description of the internal structure of the otic region except what can be seen rather imperfectly from the sectioned braincase of MCZ 3302. Apparently the internal ear region was widely open to the brain cavity opposite the two otic elements, although partial anterior and posterior ossified walls are formed by them.

*Lower jaw* (Figs. 13-15). Like the skull, this is a very stoutly built structure and is relatively broad, but shallow. As can be seen in the cross-sections figured by Williston (1916a), both external and internal walls of the jaw ramus are thick. In section, the jaw is somewhat triangular. The upper surface is broadened for the coronoid toothplate; the inner surface is essentially vertical. On the

outer surface, a longitudinal, shallow shelf is present in the region opposite the adductor fossa; this corresponds to the lower boundary of the jugal flange of the skull. The lower part of the outer surface curves gradually medially, to compensate for the dorsal width, so that most of the splenial-angular area and the lower part of the dentary are seen in a ventral rather than a lateral view. Much of the outer surface of the jaw is sculptured in a fashion similar to the skull roof, but in the posterodorsal portion of the external surface,

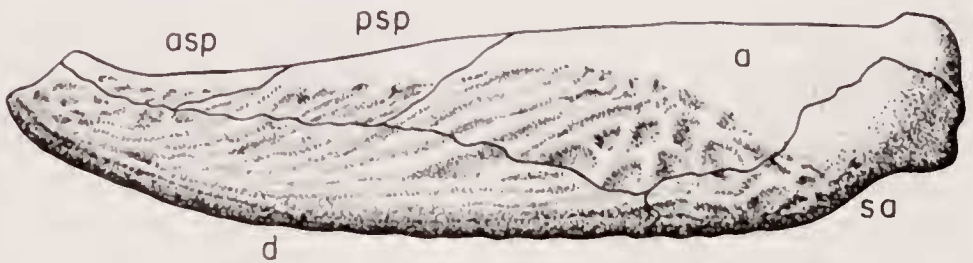


Fig. 13. Ventrolateral view of right jaw ramus, ventral margin at the top,  $\times 1\frac{1}{2}$ .

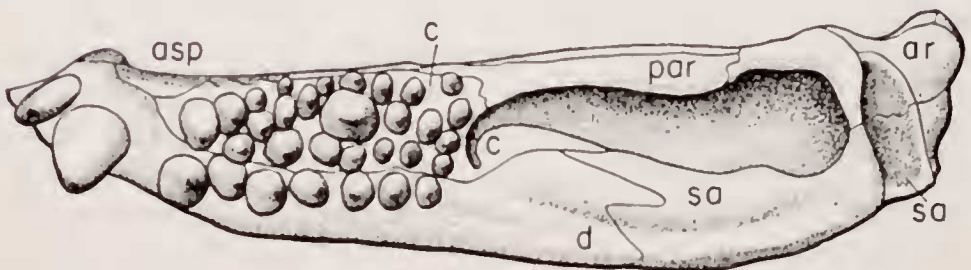


Fig. 14. Dorsal view of left jaw ramus,  $\times 1\frac{1}{2}$ .

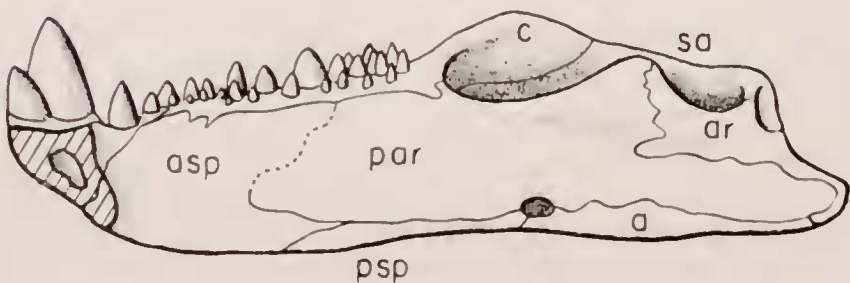


Fig. 15. Internal view of right jaw ramus,  $\times 1\frac{1}{2}$ .

from the coronoid process down to the longitudinal shelf already mentioned, the jaw (here covered by the jugal flange) is smooth-surfaced. The ventromedial margin of the lateral surface also lacks sculpture, presumably due to the fact that here, between the jaw rami, the skin was lifted free from the bone. Rather unexpectedly in such a strongly built structure, the symphysis, although stoutly fused, is of modest extent — a triangular area with a vertical posterior border and a curved anteroventral external surface. The opening of the adductor fossa is large, extending about half the length of the jaw back from the curved posterior border of the coronoid plate to the articular area. A large cavity of subcircular shape, corresponding to the Meckelian canal of reptiles, extends forward without interruption from the adductor fossa nearly to the symphyseal region. Presumably this carried in its floor the anterior part of the Meckelian cartilage.

Lateral to the opening of the adductor fossa there is an elongate coronoid process, which rises fairly rapidly from a point near the posteroexternal border of the coronoid toothplate and decreases gradually in height posteriorly. It slants gently toward the medial side above. Opposite the coronoid process there is a smaller, thin, process extending upward from the medial margin of the adductor fossa. As in the upper jaw, the articular surface is broad medio-laterally, narrow anteroposteriorly. It is gently concave in anteroposterior section. The broad posterior margin of the jaw slants nearly directly downward for a short distance below the articular surface, but then turns strongly backward to form a pronounced and broad retroarticular process, rather more developed medially than laterally. On the inner surface of the jaw there is a typical Meckelian foramen opening into the adductor fossa; this lies close to the ventral jaw margin, about a third of the jaw length forward from its posterior end. Williston (1916a) described a second, smaller, Meckelian foramen much further forward along the inner jaw surface; I have not been able to identify this small opening in the available material. Presumably a fossa for the chorda tympani was present, but I have not observed this opening.

As commonly, the dentary is the largest element of the jaw. Anteriorly, it forms most of the jaw symphysis, behind which it is exposed on the inner surface for a short distance only. Externally it occupies a large part of the surface of the ramus. Anteriorly, where it is bounded ventrally by the splenials, it occupies the greater part of this outer surface; more posteriorly, adjacent to the angular and surangular, its lower boundary retreats gradually upward. At the level of the longitudinal shelf mentioned above, the surangular

extends forward in V-shaped fashion to overlap the dentary to some degree; above this, on the coronoid process, however, the dentary succeeds in extending well backward, and forms much of the outer surface of the process, although not reaching its summit. Anteriorly, the medial boundary of the dentary descends along the outer surface of the coronoid process to extend forward along the medial margin of the lateral tooth row, where the suture lies in a marked groove.

Of the infra-dentary series, the two splenials are found in their usual position externally, occupying a modest area near the ventromedial termination of the morphologically lateral surface. The posterior splenial extends around the lower jaw margin to be exposed along a narrow ventral strip on the medial surface. The anterior splenial is more extensive in medial exposure. I have some doubts as to its boundaries, but the anterior splenial appears, as Williston figures it, to extend upward as a thin sheet over the anterior end of the prearticular to border the anterior end of the coronoid plate and gain contact with the dentary behind the anterior tooth pair; it forms the ventral third of the symphysis. The angular has its normal exposure, of considerable extent, over the posteroventral region of the outer surface; posteriorly it forms the outer part of the retroarticular process. Internally it is exposed ventrally, running forward to partially bound the Meckelian foramen. The surangular is well developed externally, where it forms much of the region of the coronoid process, excepting its highest and most anterior portion. Posteriorly it participates in the formation of the retroarticular process. Paralleling its upper jaw analogue, the quadratojugal, the surangular turns medially at the posterior end of the ramus and forms the lateral third of the articular condyle.

It is possible that the presumably primitive series of three coronoids was present in *Pantylus*, but I have not been able to distinguish sutures in available material. The coronoid area forms a large plate bounded laterally by the dentary, superficially on the medial side by the prearticular, and anteriorly by the anterior splenial. Medially, beneath the last-named elements, a thick flange of the coronoid, at right angles to the exposed portion, extends far ventrally, giving stout support to the toothplate, as figured by Broom (1913, fig. 4) and Williston (1916a, fig. 27). Posteriorly, behind the termination of the toothplate, the coronoid complex takes part in the formation of the coronoid process; it forms the inner surface of the high anterior portion of the process and is also exposed externally at its summit.

The prearticular is extensively developed. For the most part, it covers the surface of the coronoid area along the inner aspect of the jaw as a thin plate of bone; anteriorly, it appears to be covered in turn by the anterior splenial. In the middle section of its extent, it is bounded ventrally by the splenials. It forms much of the boundary of the Meckelian foramen, posterior to which it is constricted in ventral extent by the angular. Back of the coronoid plate it forms by itself the whole of the medial wall of the adductor fossa to the summit of the medial dorsal process which was mentioned earlier. Behind this point it is constricted dorsally by the articular; it extends to the posteromedial corner of the jaw as a restricted strip of bone between the articular above and the angular below.

The articular forms the medial two-thirds of the jaw articulation. Below, it descends to bound the posterior end of the adductor fossa and form part of the substance of the retroarticular process; as far as I could determine, however, it does not appear on the surface of that process. Medially it turns forward above and internal to the prearticular to form a portion of the inner wall of the adductor fossa.

Lying within the floor of the Meckelian canal for much of its extent is a thin sheet of bone, shown in the sections of Mehl (1912, fig. 4). It is somewhat broken and discontinuous in my sections, but is obviously not part of any one of the dermal ossifications lying external to it. It seems surely to be a Meckelian ossification in the lower surface of the cartilage which probably filled much of the canal.

*Dentition* (Figs. 2, 5, 7-12, 14, 15). *Pantylus* was endowed with a powerful dentition of stout but blunt teeth, both on the jaw margins and internally on broad areas of the palate and the coronoid area of the lower jaw. In section there is no trace of labyrinthine infolding of the enamel; nor is there any trace of a division of teeth into basal and distal portions, as might be hoped for in a member of a group possibly related to the modern amphibian orders (cf. Parsons and Williams, 1963). Evidence of tooth replacement was looked for, but not found. It seems clear that *Pantylus* subsisted on some type of durophagous material. A molluscan diet has been suggested by various authors. This is not unreasonable; but it is to be noted that little trace of molluscs has been seen in the beds from which *Pantylus* specimens have been collected, and probably some hard plant material formed the food supply. The massive construction of skull and jaw is reasonably to be correlated with strong masticatory movements, and great strength of the jaw muscles is indicated by the great size of the subtemporal fossae,

through which the temporal muscles descended — the breadth of these cavities being correlated with the unusual width of the temporal region of the skull.

The upper marginal teeth, particularly the more anterior ones, are somewhat tilted inward at their tips (a reverse outward slant is present in the lower anterior teeth). Three teeth are generally present on each premaxilla. The first is large and powerful and is, next to the "canine," the largest tooth in the upper jaw. Lateral to this are usually two further "incisors," somewhat smaller, but nevertheless rather longer than any of the maxillary teeth except the "canine"; the two are crowded close together and are somewhat compressed from side to side. One small and presumably young specimen shows but one tooth in this position. Immediately behind the lateral "incisor" is the powerful "canine," most anterior member of the maxillary row. Behind the "canine" is a series of cheek teeth. The first of these is little more than half the length of the "canine," and the first few following teeth are of about the same length. More posteriorly there is a gradual diminution in size. The specimen sectioned is somewhat imperfect posteriorly along the jaw margins, so that there is some question as to the exact number in the series; there are, in this specimen, certainly eight and possibly nine post-"canine" teeth. Some specimens show a larger number of cheek teeth. Williston (1916a), for example, states that there are 15 or 16 maxillary teeth (but figures only 16 for premaxilla and maxilla combined). Discrepancies in tooth counts may be due to individual variation or, quite possibly, to posterior additions to the tooth row during life.

In the marginal row of the lower jaw, there are two anteriorly-placed "incisors." The more medial of the two is the smaller, but this is, nevertheless, more powerful than any but the most anterior of the lower cheek teeth. This tooth is somewhat compressed from side to side at its base. The lateral "incisor" is of considerable size and strength, equalled only by the upper "canine." As noted earlier, this tooth is so highly developed that when the jaws were closed, it extended well up into the anterior part of the bony choanal opening (as did the median incisor to a lesser degree). Beyond the lateral "incisor" there is a slight dip in the height of the jaw rim and a gap, allowing for the passage of the upper "canine." Following this short diastema there is a series of marginal teeth, which mainly match in size the more anterior post-"canine" teeth in the maxilla. I have found but seven teeth in the post-"incisor" series in the lower jaw of the sectioned specimen,

in contrast with the higher number above, and there is relatively little diminution in size toward the back of the series.

Teeth are highly developed on the palate. I have seen no evidence of parasphenoidal teeth (found occasionally in early tetrapods). Beginning a short distance anterior to the basal articulation, the anterior ridge of the pterygoid is studded with small teeth. These are rather irregularly placed, but for most of the length of this long ridge they are essentially arrayed in two irregular rows. The vomers, lateral to the anterior ends of the pterygoids, bear a series of teeth of somewhat larger size.

The major palatal tooth assemblage is found on the extensive palatine bones. There is some irregularity in the arrangement, even between the two sides of a single individual (as that sectioned and figured), but there is, in the few palates I have seen, a uniform basal plan. Somewhat to the lateral side of the center is a very large but quite blunt tooth with an oval base and a crown slanting anteromedially. Just behind and medial to this tooth is a bare area of the palate into which, in the closed jaw position, a similarly large lower tooth is lodged. A longitudinal row of rather large teeth runs along the lateral margin of the bone; the lower marginal teeth in closure lay between this row and the marginal upper teeth. Anteromedially, a row of teeth of modest size continue backward from the vomerine series. A few teeth of a size comparable to those of the marginal row are present in front of the large central tooth, and good-sized teeth are present medial to it. About a score of teeth are present in the posterior portion of the palatal plate. They are of variable size; many are moderately large, but there is a decrease toward the angular posteromedial boundary of the palatine.

The coronoid region of the broadened upper surface of the lower jaw bears a battery of teeth, somewhat over a score in number, which correspond roughly to the palatal assemblage above. There are, however, no lower teeth to oppose those on the pterygoids or (naturally) those on the vomers. Further, the lower tooth plate is much narrower than that of the palatine, and the teeth are more closely crowded. As in the case of the palatine, there is a large, broad-based tooth centrally situated on the coronoid plate. Despite the crowding of the lower plate teeth, there remains, in the sectioned specimen, a small bare area just anterior to this tooth, in which was received the summit of the crown of the major upper plate tooth. As in the palatine plate, there is a row of stout teeth along the lateral margin of the plate, and well-developed teeth are present anterior and posterior to the major

tooth. Teeth forming a medial row are of smaller size.

Individual variations in the number and position of teeth in the palatine and coronoid toothplates are to be expected, and it was mentioned earlier that in some cases the large, centrally-placed teeth in these plates may be absent. In the sectioned specimen, upper and lower jaws were in occlusion at death, and it could be seen that there was a perfect coordination between upper and lower toothplate sets. There was never any direct opposition between an upper and lower tooth; each upper tooth fitted into a gap between lower teeth, and vice versa.

*Visceral arch elements* (Fig. 16). As attested by the presence of a pebbly sheet of dermal ossicles similar to those seen in *Tuditanus* and "*Ricinodon*" *limnophyes*, the skin between the jaw

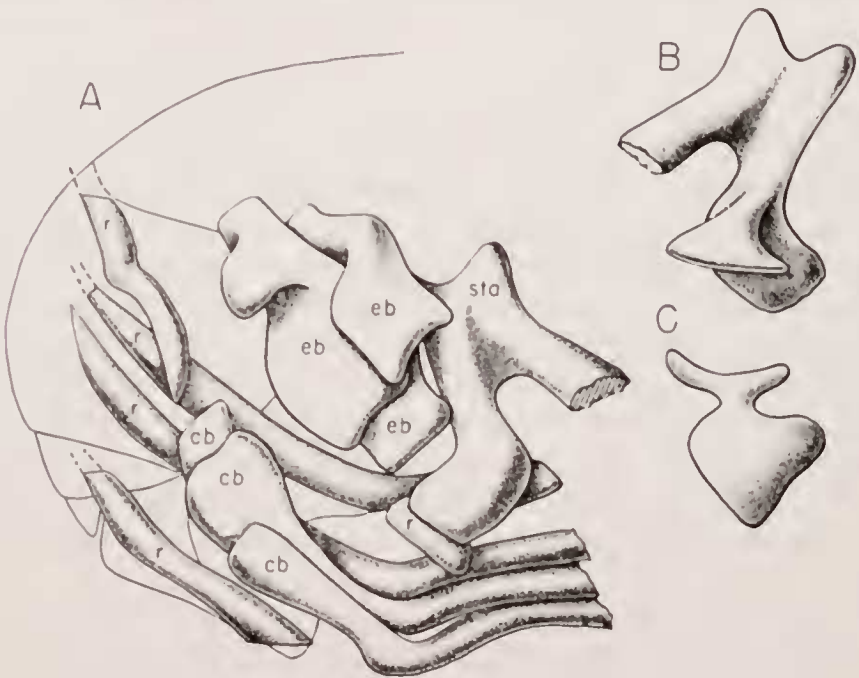


Fig. 16. *A*, Postcranial structures preserved behind left side of occiput, from reconstruction of the sectioned specimen. Outlines of the skull elements shown for orientation; *cb*, ceratobranchials, *eb*, epibranchials, *r*, rib fragments, *sta*, stapes. *B*, Stapes from anterior side, as oriented. *C*, Ventral view of main shaft of stapes. All  $\times 3$ .

rami was still present when the sectioned specimen underwent burial, and various bones were preserved in this "pocket" for fossilization. We have already mentioned the presence here of detached vomers, epipterygoids, and otico-occipital elements. Further, the first three vertebrae had been pushed forward into this

area, and ventrally a fraction of the dermal shoulder girdle is included also in the block. On the right, the sectioned block terminates directly back of the occiput and jaw articulation; on the left, however, the block extended a short distance farther back, so that there are present part of the cervical rib series and — much more interesting — part of the visceral arch series of the left side.

Fairly high up in the block, centered about behind the left otic region, are three elements which appear rather certainly to be epibranchials. These are thin-walled, incompletely ossified internally, with a spongy structure. They are essentially leaf-shaped, each with a broad distal expansion, thin anteroposteriorly; the three are closely appressed. Dorsally, each narrows somewhat to a “stem”; however, the one seen farthest to the left in the figure has a rather broad expansion at its “head.”

Separate from the presumed epibranchials and running transversely lower down in the block are three further structures, which appear to be ceratobranchials. Each consists of two contrasting segments. At the left, and slanting ventromedially, are “head” portions which resemble the epibranchials in being thin-walled, spongy internally, broad in the transverse plane, but thin and rather closely appressed, one to the other, anteroposteriorly. At their lower ends, each turns directly medially and assumes the form of a tube, thick-walled but hollow centrally. These extend for a (relatively) considerable distance to the right. They terminate somewhat irregularly; this may be due either to post-mortem damage or to the presence of cartilaginous terminations. At their distal ends each of the three narrows dorsoventrally but broadens anteroposteriorly, like flattened cornucopias.

A further visceral structure is present in the sectioned specimen, to the right of the presumed epibranchials. This is a stout element which, as preserved, begins dorsally high up just behind the lower inner portion of the occipital plate of the left supratemporal. For a short distance there are two semi-distinct “heads.” but these shortly unite to form a single, rather large structure, of rhomboidal shape in section, relatively thin-walled, and with a spongy interior. A short distance down there is a bifurcation. One branch slants sharply to the right and somewhat posteriorly; distally this ramus becomes shattered, so that nothing can be said of its extent or distal terminus in life. The other branch runs nearly directly ventrally. For a short distance it contracts, to have a relatively small diameter and good walls; beyond, it expands to a large diameter, with a spongy interior and with thin walls except toward the right and anteriorly. Anteriorly there develops a well-formed

projection, thin at its base but then expanding toward each side, giving a T-shaped section.

It seems certain that this element is a stapes, and rather surely that of the left side. In its disarticulated state there is no certainty as to its interpretation and position in life. At first thought, one would tend to interpret it in terms of the pattern common in early tetrapods and crossopterygians (cf., for example, Romer, 1956, fig. 197). On this assumption, the upper end as figured would be that associated with an ear drum (if present), the shorter branch to the right a dorsal process, the vertical processes the main shaft, with the footplate at the bottom. But various considerations suggest an alternative hypothesis — that the upper terminus is a broad footplate, that the complex lower end of the main shaft was associated with an eardrum or other auditory structure, and that the branch to the right braced the structure laterally in some fashion on the occipital aspect of the cheek (somewhat analogous to the crossopterygian opercular process). On this assumption, the posterior surface of the stapes is that seen in Figure 16B. The somewhat bifurcate nature of the presumed footplate may be due to close apposition of shaft and dorsal process, but is also slightly suggestive of initiation of the lissamphibian division of the apparatus into stapes plus operculum.

#### PANTYLUS AS A MICROSAUR

Two facts seem immediately clear: (1) *Pantylus* is closely related to microsaurs of the gymnarthrid group, and (2) neither *Pantylus* nor its microsaur relatives are reptiles or ancestral to reptiles.

The description above has, I think, made it obvious that *Pantylus* is a microsaur. It is specialized for a durophagous diet in its massive skull build, accommodation for powerful temporal muscles, and powerful dentition. Otherwise it compares readily in many regards with the contemporaneous gymnarthrid microsaurs; dentitions of intermediate type are known among Carboniferous microsaurs in Canada and Bohemia. *Pantylus* exhibits the diagnostic cranial patterns of the group, such as those which I specified in 1950 and the additional features noted by Carroll (1966) and by Carroll and Baird (1968). The most obvious feature is, of course, the presence between parietal and squamosal of a large roofing element generally termed "supratemporal." In all labyrinthodonts we find here a row of elements, including a tabular posteriorly and more anteriorly a distinct supratemporal

and, in many primitive forms, an intertemporal as well. Supratemporal and tabular are present as distinct elements in primitive captorhinomorph reptiles. Never, however, is there any growth of a large element such as the microsaurs "supratemporal." In specialized captorhinomorphs tabular and supratemporal are reduced, so that—in strong contrast to microsaurs—squamosal and parietal come in direct contact for most of their length.

In all early tetrapods there is a trend for the development from the posterior elements of the dermal roof of flanges sheathing the occipital surface. Such flanges are highly developed in *Pantylus*, particularly that from the "supratemporal." The occiput is poorly known in most microsaurs; however, a similar occipital sheathing is known in a few other cases, and "*Ostodolepis*," as figured by Case (1929), shows an even greater development of such dermal structures than that in *Pantylus*. It is highly probable that the presence of extensive dermal flanges in the occiput is a diagnostic microsaurs feature.

Typical of microsaurs (and early amphibians in general) is the rounded posterior contour of the palatal plate, in contrast with the development of the stout pterygoid flange seen in early reptiles. In various primitive amphibians we find narrow interpterygoid vacuities and a movable basal articulation of braincase and palate, in contrast to the "open" palate and fused basal articulations seen in most temnospondyls and modern anurans and urodeles. The primitive condition persists here in microsaurs in which the palate is known; *Pantylus* is in agreement with this condition.

The braincase is poorly known in most microsaurs. It is possible, although of course not certain, that the structures described above in *Pantylus* are typical of microsaurs in general. We have seen in *Pantylus* a well-developed sphenethmoid of a type widespread among primitive tetrapods and presumably typical of microsaurs in general. The basisphenoid region, again, in the presence of well-developed basiptyergoid processes and a good pituitary fossa, with adjacent openings for the internal carotids and a transverse pituitary vein, is of a primitive and generalized nature. Quite different, however, from other known primitive types is the structure of the more posterior and posterodorsal regions of the braincase. The sharp downward inclination of the anterior process of the supraoccipital is a feature not seen or expected in any other early tetrapod group. Case (1929), in "*Ostodolepis*," described such a structure. Until I discovered it in *Pantylus*, I was inclined to consider its position in Case's specimen as due to post-mortem injury. Its presence in both these forms strongly suggests that it

was characteristic and definitive of microsaur. Again, the broad sheet of bone extending independently upward from the basisphenoid in *Pantylus* finds no homologue in other ancient groups. It is difficult to imagine a brain configuration fitting this braincase structure. The downward tilt of the supraoccipital eliminates the possibility of the midbrain having extended forward into the area between these dorsal extensions of the sphenoid. If brain tissues were shielded by them, the only possibility is that the cerebral hemispheres were tilted strongly upward and backward here above the diencephalon.

The strong lateral projection of the otic bones and the near-terminal ventral position of the fenestra ovalis are unusual features, somewhat reminiscent of the Seymouriamorpha. The occipital condyles are known in several other microsaur; where seen, they appear to be essentially similar to the tripartite, *Eryops*-like condyle of *Pantylus*.

Since visceral arches are seldom reported in the older Amphibia, the epi- and ceratobranchials described above in *Pantylus* are at present of little significance in problems of early amphibian relationships. My identification of a V-shaped element as the stapes is supported by information given me by Dr. Carroll that an identical structure, likewise a presumed stapes, is present in *Ostodolepis*, and by Dr. Olson that such a structure is also present in an as yet undescribed gymnarthrid from the Permian of Oklahoma. The whole question of stapedia elements in microsaur is still an unsettled one. Since many modern amphibians have two auditory ossicles, operculum as well as stapes, there has been a tendency to look for a pair of ossicles in microsaur, as possible ancestors of the modern Lissamphibia (cf., for example, Gregory, Peabody, and Price, 1956). Shell-shaped structures seen in the ear region of gymnarthrids have been interpreted as stapedia elements, and in some cases other fragmentary materials seen in this region have been thought to be accessory auditory ossicles. I rather doubt both interpretations. As described above, the otic bones in *Pantylus* are essentially shell-shaped and separate readily from the parasphenoid and other braincase elements. The shell-shaped presumed ossicles are probably disarticulated otic bones; the fragmentary materials mentioned are not improbably remains of the adjacent hyoid apparatus.

#### MICROSAUR RELATIONSHIPS WITH OTHER AMPHIBIANS

In 1933 I provisionally united the various amphibian types possessing "holospondylous" vertebrae in a single group of Lepospondyli, using this Zittel term in an expanded sense and including

as Paleozoic components the three groups established by the Miall committee in 1875 — Nectridea, Aistopoda, and Microsauria. Study of the *Pantylus* skull neither adds to nor subtracts from the rather tenuous bonds which may possibly unite these three very diverse groups.

In addition to the more typical microsaur, such as the gymnarthrids, *Tuditonus*, and *Microbrachis*, a number of other Paleozoic lepospondyls, such as *Lysorophus*, *Molgophis*, and the “adelogyrinids,” are often united, although with some doubt, with the microsaur. Recent and current studies have done nothing to strengthen this supposed association. It is, in fact, weakened by the results of “modern” studies which show, despite my fond hopes to the contrary, that extreme reduction of the cheek elements, beyond that of the microsaur, had already taken place in the “adelogyrinids” of fairly early Mississippian times. These forms had departed at the dawn, so to speak, of amphibian evolution very far from the skull pattern of the Labyrinthodontia, while more typical microsaur, as suggested below, could have been readily derived, as regards most cranial structures, from labyrinthodonts during Carboniferous times.

If we compare the skull of such a microsaur as *Pantylus* with that of early labyrinthodonts, we find that the two agree in many features. Apart from the diagnostic change in the temporal region and greater overlap of roof elements onto the occiput, the dermal roof pattern and that of the jaw are very close to the early labyrinthodont plan. The palate, too, is similar to that of the more primitive labyrinthodonts, and even the broadening of the concave occipital condyle parallels the trend in temnospondyls. The only really distinctive skull features, apart from the “supratemporal” region, are in the dorsal development of the sphenoid, the down-turned anterior process of the supraoccipital, and the lateral extension of the otic region. As far as skull structure is concerned, there is no difficulty in deriving typical microsaur from labyrinthodonts; and, disregarding vertebral structure, the changes necessary need not, one would think, necessitate more than a fraction of Carboniferous time for their accomplishment. Typical microsaur, considering skull structure alone, could have evolved from Lower Carboniferous — Mississippian — labyrinthodonts.

I have previously (1950, etc.) suggested that microsaur may have given rise to part, at least, of the modern amphibian groups. Parsons and Williams (1963) are inclined to doubt this, citing such features as the long and slender body and feeble limbs of

many microsaurs as tending to throw them out of consideration as ancestors of the Lissamphibia. But as Carroll and Baird (1968) point out, such forms as *Pantylus* and *Tuditanus* show more sturdy body proportions and stouter limbs than most earlier described types. There is no positive proof, but I continue to believe that microsaurs are still worthy of consideration as possible ancestors of the modern orders. From time to time, most recently by Estes (1965), the rhachitomes, particularly the Dissorophidae, have been suggested as possible ancestors of part or all of the lissamphibian groups. But although Estes is inclined to consider the balance slightly tipped in favor of the rhachitomes, there seems to be little in the way of conclusive evidence.

#### MICROSAURS AND REPTILES

Certainly typical microsaurs resemble early reptiles in various ways, implying a considerable degree of parallelism if not true relationship, notably in such characters as the tarsus and the attainment of a "holospondylous" construction of the vertebral column. But I am quite unable to understand how anyone who looks even superficially at the skull can believe that any reptiles, such as captorhinomorphs, can be of microsaur descent. The pattern of the temporal region has evolved in a fashion very different from that leading to reptiles; the "supratemporal" (or tabular), reduced and soon lost in reptiles, has enlarged in spectacular fashion in microsaurs. And even in such features as the tripartite condyle, the microsaurs have gone in a direction quite at variance with that proper to reptile ancestors, which have retained and emphasized the primitive single condyle of the ancestral amphibians. It seems to me high time that this impossible theory of reptile descent from microsaurs should be given permanent burial.

I suggested at one time that possibly microsaurs, although not ancestral to reptiles, might, on the contrary, be an offshoot of primitive captorhinomorphs. I have never considered this as too probable, and now believe this to be no more worthy of belief than the opposite relationship. Sudden great expansion of a "supratemporal," already much reduced in even the most primitive captorhinomorphs, a radical shift in structure in the posterior part of the braincase away from the reptilian pattern seen in captorhinomorphs, a paralleling of temnospondyls and modern amphibians in a "last-minute" expansion of the occipital condyle — such shifts seem highly improbable indeed.

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